

Ecolab, Webworld and self-organisation

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Abstract

Ecolab and Webworld are both models of evolution produced by adding evolution to ecological equations. They differ primarily in the form of the ecological equations. Both models are self-organised to a state where extinctions balance speciations. However, Ecolab shows evidence of this self-organised state being critical, whereas Webworld does not. This paper examines the self-organised states of these two models and suggest the likely cause of the difference. Also the lifetime distribution for a mean field version of Ecolab is computed, showing that the fat tail of the distribution is due to coevolutionary adaption of the species.

Introduction

In models of evolving ecologies, a “drip feed” of mutated species are added to a simulation of ecological dynamics. As new species are incorporated into the ecology, they create new links in the food web, perturbing the system dynamics. When enough links are added, feedback loops will form, and the simulated ecology will suffer a mass extinction. Over time, the system *self organises* to a state where the introduction of new species will be balanced by extinctions, and the system diversity fluctuates around some mean value.

But what is this state that the system self organises to? The first suggestion was a *critical* state (Bak and Sneppen, 1993), characterised by long range influences of a species extinction over others in the food web. The original model of Bak and Sneppen used to illustrate this idea is no more than a cartoon. The interactions between species in this model had no relation to biological interactions. The first attempt to use some real biologically inspired dynamics was probably Ecolab (Standish, 1994), which employed the well known Lotka-Volterra equations, for which a quite a bit of theoretical information is available. This model clearly self organises to a state where speciation is balanced by extinction of average (Standish, 1999), although a variation of the model (incorporating a mechanism of specialisation) produces unbounded growth in diversity (speciation exceeding extinction) (Standish, 2002).

So is this state a critical state? One problem is that criticality in self-organised systems is only achieved in the limit

of zero driving rate — in this case zero mutation rate. Sole *et al.* (Solé *et al.*, 2002) prefer the term *self-organised instability*. Whilst I am sympathetic to this notion, I would also like to point out that *stability* is very precise term in dynamical systems theory, referring to the behaviour of the linearised system around an equilibrium point. Unstable ecosystems do not have to fall apart — the classical Lotka-Volterra (Maynard Smith, 1974) limit cycle is a case in point. Rather the notion of an ecosystem persisting in time without falling apart is captured by *permanence*, for which a few modest results are known for Lotka-Volterra systems (Law and Blackford, 1992). So perhaps self-organised impermanence would be a more accurate description.

Self organised critical systems are characterised by a power law distribution of extinction avalanches, and also a power law distribution of lifetimes. Traditionally, the presence of power law signatures in a self-organising system is taken as evidence of self-organised criticality. Newman (1997) developed another toy evolutionary model that exhibited power law spectra, with neither self-organisation nor criticality in sight. However, when the artificial constant diversity restriction is lifted in the obvious way, self-organisation reappears (Standish, 1999), and the model can also be understood as a mean field approximation of coevolutionary system that potentially admits critical behaviour.

Ecolab demonstrates power law spectra of lifetimes (Standish, 1999), with an exponent of -1. However, it has proven very difficult to measure the distribution of extinctions, as extinction avalanches overlap in Ecolab due to the finite rate of speciation. Conversely, studies of a similar model called Webworld claim an absence of any power law signatures (Drossel *et al.*, 2001). I have implemented the Webworld model using the *Ecolab* (Standish,) simulation system. I was similarly unable to see evidence of power law signatures, and propose a possible explanation.

In this paper, I show that the Fourier transform of the diversity time series is related to the lifetime distribution. Furthermore, in the limiting case of infinitesimal speciation, this transform is the distribution of extinction avalanches (extinction frequency).

Ecolab model

We start with a generalised form of the Lotka-Volterra equation

$$\dot{n}_i = r_i n_i - n_i \sum_j \beta_{ij} n_j. \quad (1)$$

Here n_i is the population of species i , r_i is the difference between reproduction and death and β_{ij} is the interaction between species i and j .

Periodically, each species i generates a number of mutant species, proportional to $n_i r_i \mu_i$, where μ_i is the mutation rate for species i . For each mutant species, the parameters r_i , β_{ij} , and μ_i are mutated from the parent species according to additive or multiplicative processes — the exact details aren't important here, but are described in (Standish, 1994).

One crucial property that is preserved by the mutation operator is *boundedness* (Standish, 2000). Boundedness ensures that population sizes in eq (1) can never exceed a particular limit.

It turns out that a necessary condition for permanence in eq (1) is that the matrix β has positive determinant (Law and Blackford, 1992). The determinant can be written as a sum

$$\det|\beta| = \sum_{\mathbf{p} \in \text{perm}(1, \dots, n)} (-1)^{s(\mathbf{p})} \beta_{1p_1} \beta_{2p_2} \cdots \beta_{np_n} \quad (2)$$

where $\text{perm}(1, \dots, n)$ is the set of permutations of the numbers $1, \dots, n$ and $s(\mathbf{p})$ is the number of swaps involved in the permutation.

All diagonal terms of β must be positive to ensure boundedness of eq (1).

Now consider permutations with one swap ($i \rightarrow j, j \rightarrow i$). If the terms β_{ij} and β_{ji} are of opposite sign (predator-prey case), then the contribution to the determinant is positive. However, if the terms have the same sign, (eg +ve, the mutual competition case, an increase in n_i causes n_j to decrease, which reduces competition on n_i , reinforcing the original change) then it describes a positive feedback loop between species i and j .

Likewise, it can be seen that the term $T = (-1)^{s(\mathbf{p})} \beta_{1p_1} \beta_{2p_2} \cdots \beta_{np_n}$ describes an $s(\mathbf{p})$ feedback loop through the ecosystem, which is a negative feedback loop if $T > 0$, and a positive feedback loop if $T < 0$. The necessary condition for permanence can be interpreted as saying that negative feedback loops must dominate over positive feedback loops for the ecosystem to be permanent.

As species are added to the system through speciation, new links are added to the foodweb at random. The chance of a positive feedback loop forming increases dramatically as the foodweb approaches its percolation threshold (Green and Klomp, 1999). Once this happens, an extinction avalanche is almost certain. The twin pressures of speciation and extinction through impermanence oppose each other leading to a state where the food web lies on its percolation threshold. Newth *et al.* (2002) examined the scaling

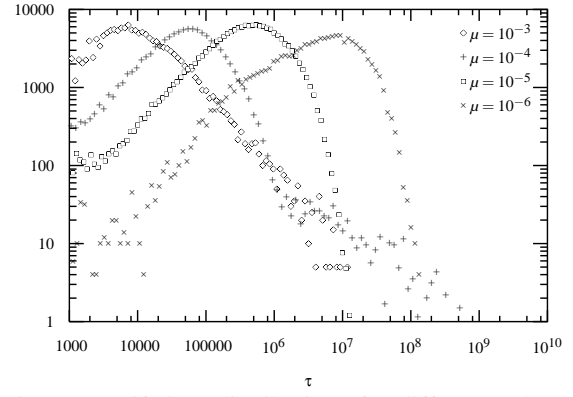


Figure 1: Lifetime distributions for different values of the maximum mutation rate μ in Ecolab. Histograms have been scaled so that the peaks are comparable in size.

structure of the Ecolab model, and observed the critical behaviour here. This is the strongest evidence yet that Ecolab self-organises to a critical state.

Plots of the lifetime distribution for several different values of the maximum mutation rate (mutation rates in Ecolab are allowed to vary, but can never exceed the maximum value) are shown in figure 1. These can be compared with other published data, such as (Standish, 1999). At higher mutation rates, the distributions exhibit a power law tail with exponent -1 . As the mutation rate is turned down, the power law tail disappears, leaving a lognormal distribution. It is unclear whether the power law has disappeared altogether, or whether with the collection of more data it will be resolved out of the noise at the base of the graph.

Relationship between diversity time series and lifetime distribution

When a species becomes extinct, it may trigger secondary extinctions in other species, in a chain of extinctions known as an *extinction avalanche*. In the Bak-Sneppen model, these avalanches follow a power law distribution in avalanche size with exponent -1 . However, it only becomes meaningful to discuss avalanche size in the limit of infinitesimal mutation rate, as otherwise the extinction avalanches overlap each other. In the Ecolab case, speciation occurs continuously, as do the resulting extinctions. More interesting is to discuss the frequency spectrum of extinctions, obtained by Fourier transforming the extinction time series. Diversity (number of species in the ecosystem at any point in time) is simply the difference between the speciation and extinction time series — in the infinitesimal speciation limit, the diversity spectrum is identical to the extinction spectrum.

The diversity time series can be written as a sum over speciation events s_j and associated lifetimes τ_j :

$$D(t) = \sum_j \Theta(t - s_j) - \Theta(t - s_j - \tau_j), \quad (3)$$

where

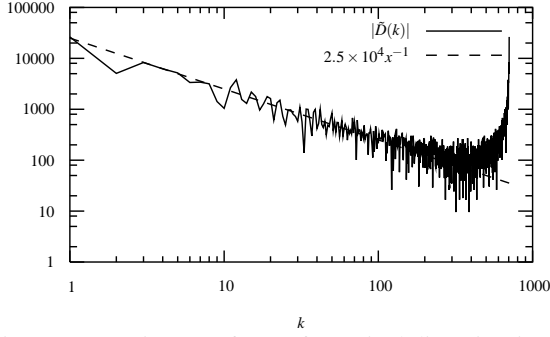


Figure 2: Fourier transform of a typical diversity time series in Ecolab showing hyperbolic behaviour.

$$\Theta(x) = \begin{cases} 0 & x < 0 \\ \frac{1}{2} & x = 0 \\ 1 & x > 0 \end{cases}$$

is the usual Heaviside step function. Taking the Fourier transform of this (and ignoring constant factors):

$$\tilde{D}(k) = \sum_j \exp(iks_j) \frac{1 - \exp(ik\tau_j)}{ik}. \quad (4)$$

Now we assume that speciation events occur every timestep (ie $s_j = j$), and that the lifetimes τ_j are sampled from a normalised lifetime distribution $T(\tau)$. Integrating over this distribution yields:

$$\tilde{D}(k) = \sum_j \exp(ikj) \frac{1 - \tilde{T}(k)}{ik} = \frac{1 - \tilde{T}(k)}{(1 - e^{ik})ik}. \quad (5)$$

Now, if $\lim_{\tau \rightarrow 0} T(\tau) < \infty$, then $\tilde{T}(k) \rightarrow 0$ as $k \rightarrow \infty$. So we can predict that asymptotically,

$$|\tilde{D}(k)| \sim k^{-1} \text{ as } k \rightarrow \infty \quad (6)$$

As $k \rightarrow 0$, $1 - e^{ik} \sim -ik$; $1 - \tilde{T}(k) \sim \langle \tau \rangle ik$, where $\langle \tau \rangle$ is the mean of $T(\tau)$. Even though a power law lifetime distribution would lead to an infinite $\langle \tau \rangle$, and any experiment, there is an upper cutoff to the lifetimes observed, which would reflect a finite $\langle \tau \rangle$. Therefore also $\tilde{D}(k) \sim k^{-1}$ as $k \rightarrow 0$. Figures 2 and 3 show $\tilde{D}(k)$ for typical Ecolab and Webworld runs respectively, and both data sets demonstrate this hyperbolic law. The power law observed in the time series spectra is uninteresting, as it is a general feature of all such stochastic processes. Adami (1998) makes a similar point in his book — that power laws in the time series spectra are necessary, but not sufficient for self-organised criticality.

Webworld

The Webworld model was introduced by Caldarelli *et al.* (1998), with some modifications described in Drossel *et al.* (2001). The model implemented here is taken verbatim from the latter paper, so I will give only a brief synopsis of the

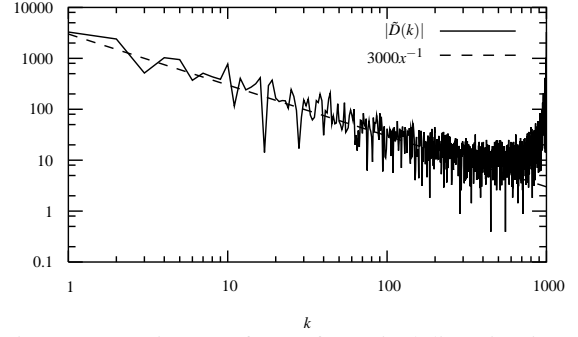


Figure 3: Fourier transform of a typical diversity time series in Webworld showing hyperbolic behaviour.

model here. The source code is available as part of the *EcQlab*¹ software suite.

Webworld has a population dynamics which is a generalisation of the Lotka Volterra dynamics (eq 1) used in Ecolab:

$$\dot{n}_i = -n_i + \lambda n_i \sum_j g_{ij}(t) - \sum_j n_j g_{ji}(t). \quad (7)$$

This equation is called a *functional response* equation. λ is a model parameter called *ecological efficiency*, and usually taken to be $\lambda = 0.1$. $n_0 = R/\lambda$ is a special species, called the *environment*. By choosing $g_{ij}(t)n_i - g_{ji}(t)n_j = \beta_{ij}n_i n_j$, $\forall i, j > 0$ and $g_{i0} = 1$, equation (1) is recovered. However, unlike Ecolab, Webworld tracks resources, and so n_i is perhaps better interpreted as the amount of biomass represented by species i than a population size.

In Webworld, the *functional response* term g_{ij} is given by

$$g_{ij}(t) = \frac{S_{ij}f_{ij}(t)n_j(t)}{bn_j(t) + \sum_k \alpha_{ki}S_{kj}f_{kj}(t)n_k(t)} \quad (8)$$

where the *efforts* f_{ij} are given recursively:

$$f_{ij}(t) = \frac{g_{ij}(t)}{\sum_k g_{ik}(t)} \quad (9)$$

Drossel *et al.* (2001) show that allowing species to vary the amount of effort in this way is an *evolutionary stable strategy*. The $\alpha_{ij} \leq 1$ terms above represent that different species do not compete as strongly as members of the same species ($\alpha_{ii} = 1$, $\forall i$).

$$\alpha_{ij} = c + (1 - c)q_{ij} \quad (10)$$

where $0 < c < 1$ is a *competition* parameter that strongly influences the final steady state diversity of the model. The precise definition of the interaction terms S_{ij} and q_{ij} is very interesting, but not germane to the argument here.

In (Drossel *et al.*, 2001), the equations are evolved in time until the ecosystem reaches equilibrium, or until a large period of time has elapsed before another species is added to

¹<http://parallel.hpc.unsw.edu.au/ecolab>

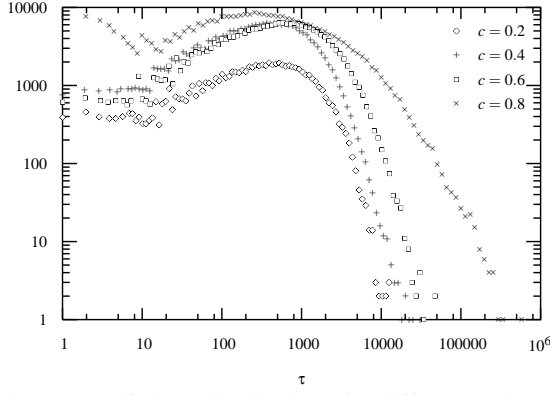


Figure 4: Lifetime distributions for different values of c for the Webworld. This is to mimic the “infinitesimal speciation rate” mentioned in relation the self-organised criticality. In this study, a single species is added periodically every 20 time units, which was chosen empirically as being sufficiently rare for the ecosystem to stabilise between speciations.

Figure 3 shows the spectrum of the diversity time series for a run with $c = 0.4$. Figure 4 shows a lifetime distribution from these runs, illustrating that the best functional form is a lognormal distribution of lifetimes. Its important to note that lognormal distributions are often confused with power law distributions (Mitzenmacher, 2003), however are distinctly different in that lognormal distributions have a mean $\langle \tau \rangle$, whereas power law distributions do not. However, as mentioned in the section describing the Ecolab model, very low speciation rates were used in this model, and it is possible that a power law tail is hidden within the noise at tail of the graph.

Quite another explanation for the absence of critical behaviour in Webworld comes from considering the dynamics of the effort coefficients f_{ij} . These are iterated within a timestep to determine evolutionary stable values — this is a model of how predators exhibiting high phenotypic plasticity might adapt to variations in food sources. It would seem to be a less plausible model of less complex organisms that might not be so choosy about their food source. Whatever the biological realism of this process, the f_{ij} coefficients describe the effective foodweb, which tends to be quite sparse and without many loops (Quince et al., 2002). Could it be that this process prevents the percolation threshold of the foodweb from being reached?

Mean Field Ecolab model

In (Standish, 1999), I introduced a mean field² version of the Ecolab model (which I dubbed Ecolab--). That model is a simple multiplicative process, which is related by log-

²Some people use *mean field* to mean *panmictic*. The Ecolab model described in previously is already panmictic. By mean field, I mean that each species experiences a stochastic force that is the average of the interspecific interactions in the full model.

arithms to the standard isotropic 1D random walk process. The lifetime distribution is known as the *first-passage time* distribution in this subject, and is known to exhibit a $\tau^{-3/2}$ tail (Redner, 2001). Note that this is different from, but still compatible with, the upper bound of τ^{-1} derived in (Standish, 1999).

However, this model has a lognormal limiting distribution of population sizes n of the form:

$$p(n, t) = \frac{1}{n\sqrt{t}} \exp\left(-\frac{(\ln n - rt)^2}{4t}\right) \quad (11)$$

This distribution does not satisfy boundedness.

In order to introduce boundedness, we need to reintroduce the quadratic term into the mean field model:

$$\dot{n} = n(r - \beta n + \gamma), \quad (12)$$

where γ is an uncorrelated stochastic variable, with zero mean.

Taking logarithms $\xi = \ln n$ and applying the Ito transformation formula (Karlin and Taylor, 1981, p. 372, e.g.), eq (12) can be written as a Langevin equation:

$$\dot{\xi} = \left(r - \frac{1}{2} - \beta e^{\xi} + \gamma\right). \quad (13)$$

The extra term of $\frac{1}{2}$ comes from the effect of change of variables on the stochastic term γ . Langevin equations can be converted into a Fokker-Planck equation describing the probability distribution $w(x, t)$ that ξ has the value x at time t (Risken, 1984):

$$\frac{\partial w}{\partial t} = \frac{\partial^2 w}{\partial t^2} - \frac{\partial}{\partial t} \left(r - \frac{1}{2} - \beta e^x\right) w \quad (14)$$

Taking the Laplace transform of equation (14) yields a second order homogeneous ordinary linear differential equation:

$$\frac{\partial}{\partial x} \left(w'(x, s) - \left(r - \frac{1}{2} - \beta e^x\right) w \right) + s w = 0. \quad (15)$$

The full time dependent equation doesn't appear to be amenable to analytic treatment, however the time independent equation ($s = 0$) can be reduced to a 1st order ODE. Let

$$y(x) = \exp\left(\left(r - \frac{1}{2}\right)x - \beta e^x\right) \quad (16)$$

$$y'(x) = \left(r - \frac{1}{2} - \beta e^x\right) y(x) = g(x) y(x), \quad (17)$$

and write $w_0(x) = w(x, 0) = y(x)v(x)$. Substitute this into equation (15), and one obtains:

$$\begin{aligned} \frac{d}{dx}(y v') &= 0 \\ v(x) &= A_0 \int^x \frac{dx'}{y(x')} + A_1 \\ &= A_0 (-\beta)^{r-\frac{1}{2}} \Gamma\left(\frac{1}{2} - r, -\beta e^x\right) + A_1 \end{aligned} \quad (18)$$

where $\Gamma(a, x)$ is an incomplete gamma function (Abramowitz and Stegun, 1965, 6.5.3), and A_j are constants of integration. Substituting this into the expression for $p(n, 0)$ yields:

$$p(n, 0) = \frac{1}{n} w(\ln n, 0) = n^{r-\frac{3}{2}} e^{-\beta n} \left(A_1 + A_0 (-\beta)^{r-\frac{1}{2}} \Gamma\left(\frac{1}{2} - r, -\beta n\right) \right) \quad (19)$$

From the series $\Gamma(a, x) \sim \Gamma(a) - \frac{x}{a} + \frac{x^2}{a+1} \dots$ (Gradsteyn and Ryzhik, 1980, 8.354), one can see:

$$p(n, 0) \sim n^{r-\frac{3}{2}} e^{-\beta n} \left(A_0 (-\beta)^{r-\frac{1}{2}} \Gamma\left(\frac{1}{2} - r\right) + A_1 \right) + \frac{A_0}{n(r-\frac{1}{2})} e^{-\beta n} \quad (20)$$

which is normalisable if and only if $r > \frac{1}{2}$ and $A_0 = 0$. We may therefore set $w_0(x) = y(x)$.

The asymptotic behaviour at large times translates into the the small s regime. We can compute $w_1(x) = \frac{\partial w(x, s)}{\partial s} \Big|_{s=0}$ by differentiating eq (15) with respect to s .

$$\frac{d}{dx} (w'_1 - (r - \frac{1}{2} - \beta e^x) w_1) + w_0 = 0 \quad (21)$$

to which the solution is:

$$w_1(x) = w_0(x) \left(A_1 + \int^x \frac{1}{w_0}(x') \int^{x'} w_0(x'') dx'' \right). \quad (22)$$

The innermost integral can be evaluated, the answer being (Abramowitz and Stegun, 1965, 6.5.2)

$$\int^x w_0(x') dx' = \beta^{-r+\frac{1}{2}} \gamma(r - \frac{1}{2}, \beta e^x) \quad (23)$$

with γ being another of the incomplete gamma functions. This can be represented as a series (Gradsteyn and Ryzhik, 1980):

$$\int^x w_0(x') dx' = \beta^{-r-\frac{1}{2}} \sum_{n=0}^{\infty} \frac{(-1)^n (\beta e^x)^{r-\frac{1}{2}+n}}{n! (r - \frac{1}{2} + n)} \quad (24)$$

Performing the integral on each term of the series yields:

$$w_1(x) = w_0(x) \times \left(A_1 + \exp(\beta e^x) \sum_{n=1}^{\infty} \sum_{j=0}^{n-1} \frac{(-1)^j \beta^j e^{jx}}{j! n(r - \frac{1}{2} + n)} + E_1(\beta e^x) \right) \quad (25)$$

where $E_1(x)$ is the exponential integral (Abramowitz and Stegun, 1965, 5.1.1).

Interestingly, for the special case $r - \frac{1}{2} \in \mathbb{Z}^+$, the result can be expressed as a finite series. It might seem that r can

be chosen to any value by scaling the time dimension without loss of generality, however that is not the case, as the timescale is already set by the variance of the stochastic term γ in eq. (12).

Considering the special case $r = \frac{3}{2}$, and making use of the identity $\gamma(1, x) = (1 - e^{-x})$ (Gradsteyn and Ryzhik, 1980, 8.352), we have:

$$w_1(x) = w_0(x) (A_1 - \beta^{-1} e^{-x} - \Gamma(-1, \beta e^x)) \quad (26)$$

To compute the asymptotic form of the lifetime distribution, we make use of *first passage theory* (Redner, 2001). The first passage probability $F(n, t|n_0)$ of the population having value n , given a starting value n_0 at $t = 0$ is related to $p(n, t|n_0)$:

$$p(n, t) = \delta(t) \delta(n - n_0) + \int_0^t F(n, t - t'|n_0) p(n_0, t'|n_0) dt' \quad (27)$$

Taking the Laplace transform, and rearranging gives us

$$\tilde{F}(n, s) = p(n, s) / p(n_0, s) \quad n_0 \neq n \quad (28)$$

(as we're not interested in the $n = n_0$ case). For concreteness, let $n_0 = 10$ and $n = 1$, as is taken in the case of Ecolab experiments computing the lifetime distribution (Fig. 1). The asymptotic form can be computed directly from $F(n, s)$:

$$\tilde{F}(n, 1/\tau) = \int_0^\infty e^{-\tau t} F(n, t) dt \sim \int_0^\tau F(n, t) dt \quad (29)$$

$$F(n, \tau) \sim \frac{\partial}{\partial \tau} \tilde{F}(n, 1/\tau) \quad (30)$$

$$= - \frac{p(n_0, 0) \frac{\partial p(n, s)}{\partial s} \Big|_{s=0} - p(n, 0) \frac{\partial p(n_0, s)}{\partial s} \Big|_{s=0}}{\tau^2 p(n_0, 0)^2}$$

Unless the numerator vanishes, the long time tail will obey a τ^{-2} power law. Substituting equations (16) and (26) yields for the case $r = \frac{3}{2}$:

$$F(n, \tau) \sim \frac{e^{2\beta n_0}}{\tau^{-2}} \left(\frac{1}{\beta n_0} - \frac{1}{\beta n} + \Gamma(-1, n_0) - \Gamma(-1, n) \right) \quad (31)$$

Since $\Gamma(-1, n) > \Gamma(-1, n_0)$ for $n < n_0$, this derivative term is negative. It seems unlikely to vanish for any value of $r > 0$, however this will need to be checked numerically.

This result is interesting. The mean field model can be considered as a neutral model, in the sense of the neutral shadow models proposed by Bedau and Packard (Bedau et al., 1998). An observed excess of lifetimes over the mean field case (in Fig 1 a τ^{-1} distribution is observed) would represent coadaptation by the species in the ecosystem.

Conclusion

In this paper, I consider the question of self-organised criticality in a couple of evolutionary ecology models (Ecolab

and Webworld). In spite of their similarity, only Ecolab appears to self-organise to criticality, whereas Webworld's self-organised state appears to be noncritical, in agreement with Webworld's creator's statements.

Whilst it is possible that experiments have not been run long enough to observe critical behaviour, a more likely explanation is organismal plasticity in Webworld prevents long range interdependence of species in the foodweb from building up.

A mean free approximation to the Ecolab model is solved, and the lifetime distribution from this model is expected to have a τ^{-2} asymptotic behaviour. The fact that the real Ecolab model appears to have a τ^{-1} asymptotic behaviour hints at adaption occurring within that system.

Finally, the spectral density of the diversity time series (which is related to the distribution of extinction avalanches) is expected to have a $1/f$ behaviour, regardless of the underlying process, so this should not be taken as evidence of self-organised criticality.

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